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THE ORIGIN OF CORN

IV. PLACE AND TIME OF ORIGIN

BY

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In regard to the origin of this plant, although there has never been room for reasonable doubt, there have been those who fancied there was room for argument. America is clearly and beyond question the native country of Indian corn. Yet, from the commencement of its history, writers have not been wanting to contest this point, and to claim for it an Eastern origin. The weight of authority and of argument so entirely preponderates in favor of its American origin, that it is scarcely worthwhile, in a work aiming to be useful rather than learned, to waste the time of the reader with idle and unprofitable speculation. —EDWARD ENFIELD (10).

This statement which appeared almost a century ago in an otherwise undistinguished work is as true today as it was then. We supposed when, some twenty years ago, we wrote our monograph on the origin of Indian corn and its relatives (31) that there was one question — its place of origin, America or the Old World — which had been answered once and for all. It turns out that we were wrong; for although our monograph stimulated much useful interest in the problem of the origin of maize, it also opened a veritable Pandora's box of unrestrained speculation on certain aspects of the problem. It has, as a consequence, become necessary once again to review the evidence pertaining to the question of corn's place of origin.

Among the herbalists and early botanists who gave their attention to maize, there were a number who regarded it as a plant of Old World origin (cf. 30). The evidence which de Candolle (7) marshalled to support his conclusion on the American origin of maize was so convincing that the problem was then generally regarded as solved. But several times in this century the question of an Asiatic origin or of a pre-Columbian distribution of maize in Asia has been raised. Following the discovery of a previously unknown type of endosperm, "waxy," in a variety of Chinese maize, Collins (9) suggested, despite Laufer's (23) earlier conclusion to the contrary, that maize may have been known in Asia before the discovery of America. More recently Anderson has, on several occasions (1, 2), suggested the possibility of an Asiatic origin of maize or of its prehistoric spread to Asia, and, in a joint paper with Stonor (38) describing some collections of maize from Assam, reached the conclusion that "maize must either have originated in Asia or have been taken there in pre-Columbian times."

The conclusions of Stonor and Anderson were welcomed by the "diffusionists," a school of geographers, anthropologists and others who professed to see in art forms, myths, and other cultural traits, including the use of plants, great similarities between Asia and America and who, for reasons which are not at all clear to us, are apparently determined to prove that all of these traits diffused from a common center. So far as plants are concerned the diffusionists' theses have had the support, especially of Carter (8), Heyerdahl (15), and Sauer (37), all of whom have regarded the conclusions of Anderson or of Stonor and Anderson as supporting the idea of pre-Columbian, trans-Pacific diffusion.

Diffusionists may also have found encouragement in Hatt's (14) fascinating study of American and Indonesian folklore which showed some remarkable similarities between the two, especially with respect to various versions of the Corn Mother myth. For example, the origin of cultivated plants from a sacrificed child, an important motif in Indonesia, is also conspicuous in Peruvian mythology. Nevertheless, Hatt was compelled to conclude that if agriculture and myths reached America across the Pacific Ocean this must have taken place not all at once but at different times, He did not suggest diffusion in the opposite direction nor did he consider it a possibility, as Sauer seems to have, that a Corn Mother myth could have been diffused except as it accompanied the spread of a grain.

The idea of a pre-Columbian interchange of plants between the Old World and the New was virtually demolished by Merrill (33). He showed that there is not only a lack of tangible evidence for such prehistoric diffusion but also that the presence of American plants in Asia soon after the discovery of America is easily and reasonably accounted for by the early Portuguese trade route established in 1500 from Brazil to Goa by way of the Cape of Good Hope.

So far as maize is concerned, the case for its pre-Columbian occurrence in Asia, never a very convincing one, was considerably weakened when Mangelsdorf and Oliver (30) showed that the Assamese maize described by Stonor and Anderson is not at all unique and has close counterparts in Colombia and other parts of South America. The case has recently been weakened still more by new evidence presented by Ho (16) who, after a searching study of Chinese historical sources, concluded that maize was introduced into China early in the sixteenth century arriving there by both overland and maritime routes. He states:

Summing up the introduction of maize into China, we may say that maize was introduced into China two or three decades before 1550; that it was probably introduced by both the overland and maritime routes; that there is little reason to justify Laufer's far-reaching conclusion, especially in the light of the introduction of other New World plants, that in the dissemination of food plants 'a land route is preferred over a sea route as their way of propagation'; and that, barring a sensational discovery in Chinese sources clearly indicating a pre-Columbian introduction, Chinese maize as a topic for anthropological speculation should be closed.

Sutô and Yoshida (39) were doubtless unaware of Ho's paper when they concluded, on the basis of decidedly meager evidence, that one of the types of oriental maize, Persian, described by them must have had an extensive pre-Columbian distribution in parts of Asia. They also favored Anderson's suggestion (2) that corn originated in Asia perhaps as an amphidiploid of a five-chromosome species of *Coix* or *Sorghum*. They were apparently unaware also of the discovery by Barghoorn *et al* (4) of fossil maize pollen in the Valley of Mexico almost identical with that of modern maize pollen. This discovery, to be discussed in more detail later, virtually proves the American origin of corn and rules out the possibility of an Asiatic origin.

Pre-Columbian Corn in Africa?

The confusion which can result from what Enfield has called "idle and unprofitable speculation" is nowhere better illustrated than in Jeffreys' (20) acceptance of that part of the Stonor-Anderson thesis which holds that, if maize did not originate in Asia, it must have been taken there in prehistoric times.

Jeffreys (17) had earlier assembled extensive historical references purporting to show that there had been Arab-Negro contacts with the Americas beginning about 900 A.D. and that maize had been introduced into Africa before 1492. When Goodwin (12) described potsherds

from Ife in Nigeria, apparently decorated by rolling a maize cob over wet clay, Jeffreys (18) proceeded to date the introduction of maize into the region in Africa represented by Ife at 1000–1100 A.D.[1], a date slightly earlier than the one which he had arrived at on the basis of other evidence (19). He then showed by linguistic and historical evidence how it might have spread from Africa to Asia (20).

To analyze Jeffreys' arguments in detail would seem to serve no useful purpose until it should first become clear: (A) that the impressions on the African pottery are unmistakably those of maize[2]; (B) that they are unmistakably pre-Columbian. Unless these two facts can be clearly established, we prefer to agree with Goodwin's recent statement (in a letter) which he has kindly given us permission to quote:

. . . and am of the opinion that not all of this pottery was decorated by rolling a maize cob over the surface. I have no evidence from that or from any other source suggesting that maize reached Africa in Pre-Columbian times.

Pre-Columbian Maize in Europe?

Finan (11), in a study of the maize illustrated and described in the herbals, concluded that there were two

[1] Weatherwax erroneously attributes to Goodwin the idea of a pre-Columbian introduction of maize into Africa. Goodwin carefully avoided drawing such a conclusion.

[2] We have not been able to obtain specimens of the African potsherds for examination but, since this was written, we have seen photographs of one of them displayed at the Tenth International Congress of Genetics in Montreal by Dr. W. R. Stanton of Nigeria. There is little doubt that this impression is of a maize cob since the paired arrangement of the spikelets is clearly shown. But Stanton, like Goodwin, regards these impressions as post-Columbian and states that he is in general agreement with Porteres (35) who, after carefully reviewing the evidence presented by Jeffreys, Mauny, and others, concluded that maize reached Africa in the sixteenth century by two routes: a flint corn by way of the Mediterranean and the Nile; a soft [probably dent] corn by way of the coast of Guinea.

distinct types: the first, characterized by conspicuous prop roots, was probably a tropical form introduced into Europe from the Caribbean area soon after 1492; the second, which lacks prop roots but sometimes has numerous tillers, is similar to the Northern Flints of eastern North America and appears to have been well known in Europe within 50 years after America's discovery. He (as well as Anderson in the preface to Finan's work) raised the question whether it could have been introduced into Europe by the Norsemen before 1492. Finan also speculated on the reason for the common belief among the herbalists that corn came to Europe from the Orient,

Sutô and Yoshida have gone even further than this in their unqualified assertion that the Aegean type, from which they believed the European maize to be derived and which was first described by Anderson and Brown (3), was, like the Persian, diffused throughout the Old World before 1492.

Corn's Rapid Spread after 1492

If all of these various assertions about pre-Columbian maize in the Old World were true, maize must have been about as widely distributed there as it was in America. Why then did it not leave a single tangible record of any kind of its presence? Why did corn cause such wonderment to sixteenth century students of plants if it had already been known for several centuries or more?

Underlying all of the speculations on pre-Columbian maize in Asia, Africa, or Europe is one common assumption: that corn could not have spread rapidly enough after 1492 to reach all of the places where it was known a generation later. This is not only a highly unreliable premise but also, we think, a presumptuous one for it places arbitrary limits, not justified either by history or

by contemporary experience, on mankind's capacity to spread, through trade and other means, the world's products. So far as Europe and Africa are concerned, the early post-Columbian occurrence of maize is explained quite satisfactorily by Wright (46) who showed how the Moors, after being partially expelled from Spain between 1499 and 1502, took maize with them to Tangier and the north African coast whence it rapidly spread to that part of the world which lay around the Mediterranean Sea, i.e., Turkey, Syria, and Egypt. Wright explains further that the name "Turk" in England during the sixteenth century was often used indiscriminately with "Moor" to indicate a Moslem. It seems probable, therefore, that maize at one period was obtained more easily in western Europe from the Moslem regions of the Mediterranean than from the West Indies and hence was known to the English as "Turkey corn" (both Egypt and Syria were then parts of Turkey) and to the Italians as *grano turco.*

Perhaps the belief, held by a number of the herbalists, that maize came from the East was based on nothing more than the fact that its common name seemed clearly to indicate an eastern origin. Some recent modern conclusions regarding its origin have had little more foundation in fact.

The Place of Origin in America

The discovery by Barghoorn *et al* (4) of fossil pollen in the Valley of Mexico seems now to have established the origin of corn in America beyond question but it still leaves open the problem of where in America maize was first domesticated.

The fossil pollen also proves without doubt that wild maize once grew in the Valley of Mexico. But the fact that maize pollen was found in the drill core only at great depths (below 69 meters) and then was absent until it

appeared again at the upper levels (above 3.6 meters), probably after the establishment of agriculture, suggests that the early fossil maize was that of a colony which became extinguished, perhaps through volcanic action. However, if wild maize grew in one Mexican valley it may well have grown in others and in similar sites in other regions.

Archaeological maize from caves in Mexico and New Mexico—some of it not far removed in its characteristics from wild corn—also points to an early center of domestication in Mexico. Furthermore, the oldest archaeological corn so far discovered in South America—that described by Bird (5) from Huaca Prieta—is later than the earliest corn from either Bat Cave or La Perra Cave and is more advanced in its development. Finally, anthropologists now tend to believe that the prehistoric cultures of America had their beginnings in Middle America and spread from there to South America (45).

For all of these reasons, Mangelsdorf concluded several years ago (26) that "Maize undoubtedly had at least one center of origin in Middle America."

This conclusion is, of course, directly contrary to our earlier one (31) that maize had its origin in the lowlands of South America—an assumption based on the fact that pod corn, which we then regarded and still regard as the ancestral form, was repeatedly encountered there and was apparently unknown in Mexico and Central America. And then, too, with teosinte disposed of as a hybrid of maize and Tripsacum, there no longer seemed to be any compelling reason for looking to the region where teosinte is native as the center of origin of maize. We have never been convinced, as Weatherwax has apparently been (41, 42, 43), that corn's center of origin must coincide with the center of diversity of its relatives, teosinte and Tripsacum.

In spite of the recently discovered evidence for a Middle American origin of cultivated maize—one which has been favored on the basis of other evidence not only by Weatherwax but also by Kempton and Popenoe (21), Kuleshov (22), Meade (32), and Vavilov (40)—we are not yet ready to rule out completely the possibility of an independent center of origin somewhere in South America although our earlier idea of a single origin in the lowlands of South America has now been abandoned.

There are still too many facts which are not completely explained by the assumption of a single origin in Middle America. Among these are: (a) the great diversity of corn in the highlands of Peru; (b) the fact that all of the known pericarp colors of corn occur in one department, Ancash, of Peru (13); (c) the frequent occurrence of pod corn in valleys on the eastern slopes of the Andes; (d) the high incidence of the tu^h gene in Peruvian corn (27); (e) the occurrence in Peru of a primitive race, Confite Morocho, which could conceivably be the progenitor of all of the other known primitive races of the hemisphere (13). So far as the evidence from living corn varieties is concerned, it still points strongly to a South American center in the highlands of Peru, Bolivia and Ecuador and, were it not for the conflicting evidence from fossil pollen and archaeological maize, we should unhesitatingly continue to assume that corn had its origin in South America.

An obvious solution to this dilemma is to assume that maize has been domesticated more than once. Such an assumption would not be radically new. We (31) have previously pointed out that five of the cultivated plants common to Middle America and South America—squashes, beans, tomatoes, amaranths, and cotton—were represented in the two regions by different species or subspecies. There is now evidence that this may have been

true also of corn. There are at least three different primitive races of maize in Peru today (13); two in Colombia (36); and four in Mexico (44). Precursors of two of the Mexican races, Nal-Tel and Chapalote, which in their characteristics are not far removed from wild corn, have been identified in archaeological collections from caves in northeastern Mexico (29) and northwestern Mexico (28). This shows that even in quite early stages of domestication there were already distinct types of corn. One conclusion which might be drawn at this time is that wild corn occurred sporadically in restricted sites in the mountainous region of this hemisphere: in Bolivia, Ecuador, and Peru in South America and in Guatemala and Mexico in Middle America. Once agriculture had been invented and maize domesticated it may have been domesticated repeatedly by the American Indians wherever it was found. Such a conclusion might require modification at any time as the result of the discovery of new archaeological evidence, especially from South America.[3]

In this connection mention should be made of the hypothesis of Birket-Smith (6), based largely on linguistic evidence, that maize originated in Colombia, perhaps in the lower Rio Magdalena Valley. In Colombia there are

[3] Since this was written a study (still unpublished) of the most recent find of archaeological maize from a site in the Ica Valley on the coast of Peru shows that the predominating type of corn is remarkably uniform and is similar, if not identical, to the prehistoric precursor of the still existing Mexican race, Chapalote. Some of the Ica ears, however, show various modifications which can be attributed to introgression from a race of popcorn, Confite Morocho, which is still found in parts of Peru, especially in the Department of Ayacucho. It now appears that the great diversity of maize in Peru had its beginnings when a prehistoric popcorn from Mexico hybridized with the Peruvian popcorn. Whether the Peruvian popcorn was already in cultivation when the Mexican race was introduced cannot be determined from the evidence now available. Additional archaeological evidence from the Peruvian highlands may shed new light on this problem.

names, some of which are regarded as "primitive," associated with maize, its culture and uses, which have affinities with those of Central America, Ecuador, Peru, Venezuela, and the South American lowlands. Roberts *et al* (36) have suggested that such a situation might have developed if this region had been not a center of origin but a crossroads in which the cultures of Central America, the Andean highlands, and the South American lowlands converged. That northern Colombia was definitely a crossroads region is now generally accepted by anthropologists. Evidence from a study of Colombian races of maize tends to support this interpretation. Other aspects of the case for a Colombian origin have been reviewed by Mesa Bernal (34).

The Time of Origin

The fossil maize pollen of Mexico, presumably that of a wild corn, is assigned, on the basis of systematic changes in the frequency of other types of associated pollen, to the last interglacial period. Recent estimates place this at 80,000 years or more ago. There is no reason to doubt that wild maize is much older than this.

The origin of cultivated maize is, of course, much more recent. The oldest archaeological specimens so far studied, those of Bat Cave in New Mexico, are dated by Libby's radiocarbon determinations of associated charcoal at 5,600 years. There is a possibility that the prehistoric maize and charcoal are not contemporaneous; that the charcoal is a residue of fires built by itinerate campers long before the cave was occupied by maize-growing people. This date, however, is not inconsistent with those from other sites. The oldest corn from La Perra Cave, dated by radiocarbon determination of associated vegetal remains at 4445 years, is by no means as primitive as the earliest Bat Cave specimens. The oldest

archaeological maize from Swallow Cave, similar to the earliest Bat Cave material, has not been dated but the fact that it occurred in levels 13 and 14, seven feet below the surface, suggests a very substantial age. The pre-pottery corn from Tm C 247, a site excavated by MacNeish (24, 25), some of which is similar to the Bat Cave corn, has been tentatively dated at 3945 years. The oldest corn from Huaca Prieta in Peru, dated about 2900 years, is already well advanced in its development over the earliest Bat Cave corn.

The evidence, so far as it goes, is consistent with the conclusion that corn was first domesticated about 5000 years ago or perhaps a millennium or more still earlier. How, even in this length of time, could the primitive corn, with which domestication began, have evolved into the highly developed varieties of today such as the Corn-Belt corn of the United States with its magnificent ears or the spectacular large-seeded flour corn of the region of Cuzco, Peru? This is a question to which we hope that the earlier papers in this series will have given, at least, some of the answers.

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THE ORIGIN OF CORN

V. A Critique of Current Theories

BY

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In the previous papers in this series (22, 23, 24, 32), we have reviewed the objections to and the evidence supporting our tripartite theory on the origin and evolution of corn. We have shown that the factual evidence for some parts of this theory has increased substantially during the last two decades, and that nothing has yet come to our attention which completely rules out any part of it.

The hypothesis that the original corn was a type of pod corn is all but proven by archaeological evidence and by a genetic reconstruction of the ancestral form (15, 16, 17, 19, 20). Because of the discovery of fossil corn pollen in Mexico, the view that corn originated in South America is less satisfactory now than it was twenty years ago, but the hypothesis of a South American origin is not yet completely untenable since research on some phases of this problem, such as that on fossil pollen, has only begun.

The evidence that teosinte (*Zea mexicana*) originated as a hybrid between corn and Tripsacum is decidedly stronger now than when the hypothesis was first presented and, contrary to opinions of several other workers, there is no sound evidence against the hypothesis. We have always recognized that this part of the tripartite theory cannot easily be tested. We have never consid-

ered the probability to be great that a "good" teosinte could be synthesized by hybridizing corn and Tripsacum in experimental cultures, and we have given reasons for this.

The recent evidence is decidedly in favor of the view that introgression between corn and teosinte has been frequent and that it has been effective in producing innumerable new varieties and forms, both ancient and modern. We now consider that this third part of the tripartite theory is almost an established fact.

It should be clear from the contents of previous papers in this series that we consider the tripartite theory to be better supported by factual evidence than any other explanation of the origin of corn proposed up to the present. The fact that we are still committed to the tripartite theory, however, should not prevent us from considering alternative theories and this we shall attempt to do objectively, if briefly, in this final paper.

The Papyrescent (*Semivestidos*) Theory

This is no more than a slight modification of the pod-corn theory. Andres (1) discovered in Argentine maize a type which superficially resembles a weak form of pod corn. Apparently unaware that Bonvicini (5) in Italy had described this character many years earlier and had given it the name "palee sviluppate," Andres called the type "semivestidos" and suggested that it, rather than pod corn, might be the ancestral form.

The character has recently been given still a third and probably more appropriate name "papyrescent" by Galinat (10), whose studies show that the glumes of this type become soft and papery as they mature. Unlike pod corn, which although sometimes monstrous still represents a combination of normal characteristics found in other grasses, papyrescent is a defect in development which it

is difficult to regard as constituting the primitive form of modern corn. No archaeological specimens of papyrescent corn have been reported.

As was pointed out in the first paper in this series, Weatherwax (41), in discussing one aspect of the pod-corn theory, apparently confused papyrescent maize and a weak form of pod corn, half-tunicate. His illustration (Fig. 51) of half-tunicate maize is almost certainly a photograph of papyrescent maize.

The Corn Grass Theory

Singleton (35) has suggested that the ancestral form of modern corn is "corn grass." This anomalous type, the product of a single dominant gene, produces numerous tillers and small "ears" with a high proportion of single spikelets. Many of the kernels are partly enclosed in bracts, but the majority of these are not glumes but spathes.

He also suggested that, if a plant of corn grass were found in nature, it would not be recognized as maize and would almost certainly be regarded as a different species if not a different genus. This may be true, and it illustrates how the maize plant can be drastically changed by a single gene mutation. If corn grass were the ancestral form, a mutation at a single locus could have transformed it from a wild, almost useless, plant to the unique cereal which maize is today.

Although corn grass has some of the characteristics which we might expect to find in an ancestral form — for example, a freely-tillering habit — it lacks others, such as the regular development of prominent glumes. At the other extreme, it has characters which are not demanded of a hypothetical ancestor. One of these, single spikelets (9), represents a condition more specialized instead of more primitive than the paired spikelets of mod-

ern maize. Another, a well-developed spathe, suggests the ancestral form not of maize but of *Coix*, whose fruit case has been found by Weatherwax (39) to comprise a spathe and a segment of the rachis. Corn grass probably is, as Galinat (8) has suggested, a "false" progenitor of maize, exhibiting certain traits which might have occurred in a remote ancestor of the *Maydeae*.

Finally, the evidence from archaeological maize does not support the corn grass theory. Prehistoric maize had prominent glumes, but it did not have the long spathes of corn grass. The possibility that corn grass is the ancestral form appears to us to be remote indeed.

The Teosinte Theory

The theory that maize originated as a domesticated form of teosinte—its nearest known relative—was first proposed by Ascherson (2). Later students, notably Harshberger (12) and Collins (6), modified the theory postulating that one parent of corn is teosinte and the other is a grass now unknown. As teosinte occurs naturally only in Mexico and Central America, supporters of this theory have usually assumed that both teosinte and maize originated in that region. We (21) concluded that teosinte is the progeny rather than the progenitor of maize — the product of the natural hybridization of maize and its wild relative, Tripsacum. Teosinte, however, plays an important role in the tripartite theory, for this theory holds that the many modern varieties of maize are the product of the introgression of teosinte into maize.

Since 1939, new evidence has been presented both in support of and in contradiction to the teosinte theory.

Beadle's (4) discovery that the seeds of teosinte will "pop" when exposed to heat, shattering the hard, bony shell in which they are enclosed, shows one way in which teosinte might have been used as a food plant and weak-

ens the objection that a species so unpromising for food purposes would never have been domesticated. There is no evidence, however, archaeological, historical or contemporary, to show that teosinte was ever employed for food in this manner. When teosinte is used for food, as it occasionally is today in times of food shortage, the fruits are crushed on a metate or with a mortar and pestle, and the meal of the crushed caryopses is separated from the fragments of the bony fruit case.[1]

Langham's (13) data on the inheritance of characteristics which distinguish teosinte and maize indicate simple Mendelian inheritance for several characters and lend some support to Emerson's (unpublished) contention that a few large scale mutations could transform teosinte into maize. But the much more extensive data of Mangelsdorf (14) and of Rogers (33, 34) show that the genes which distinguish maize and teosinte are numerous and are distributed among a majority of the chromosomes. The highly significant studies of Rogers seem to have been completley overlooked by both Weatherwax and Randolph; at least they are not cited in their extensive bibliographies.

The recent studies of Barghoorn, Wolfe and Clisby (3) on fossil pollen in Mexico lend no support to the teosinte theory. Although pollen of both maize and Tripsacum was found at great depths, the pollen of teosinte occurred only near the surface in the upper levels of the drill core where maize pollen was abundant suggesting that the practice of agriculture had begun. Furthermore, the maize pollen found at the lower levels is as large as any modern maize pollen and shows no resemblance to teosinte pollen in the ratio of total diameter to the diameter of its pore. If this fossil pollen is as old as it is estimated to be — 80,000 years or more — the

[1] Personal communication from the late R. H. Barlow.

theory that maize originated from teosinte under domestication can now be safely ruled out.

Recent studies of archaeological maize, like those of fossil pollen, do not support the teosinte theory. On the contrary, they show that the earliest maize was less like teosinte, whereas some recent maize is more like it. Archaeological specimens exhibiting characteristics of teosinte, including distichous ears, single spikelets and highly lignified rachises and glumes, have been found in several sites. But these are always recent specimens and are interpreted as being products of the introgression of teosinte into cultivated maize (7, 11, 19, 20, 25).

A series of studies on the morphology of the corn ear has a bearing on the teosinte theory, because many workers who favored this theory explained the polystichous character of the corn ear as the result of the lateral fusion of several teosinte spikes. The voluminous literature on this subject was reviewed by Mangelsdorf and Reeves in 1939 (21) and more recently by Nickerson (27). The present status of the problem is that evidence for the lateral fusion of two-rowed spikes to form the polystichous ear is completely lacking; the only evidence found for fusion is the adnation of the rachis flaps (prophylls) to the main axis of the cob. It may be concluded, therefore, that the structure of the corn ear has thus far shown no evidence that corn is a descendant of teosinte.

The Theory of Common Ancestry

It appears that Montgomery (26) was the first to propose the theory of common ancestry, although he did not include Tripsacum in the alliance with corn and teosinte. Weatherwax (37) formulated the theory as we now know it, by adding Tripsacum to the two species considered by Montgomery, and he defended it in subsequent publications (38, 40, 41, 42). Randolph (28, 29)

agreed with Weatherwax, with reservations; he still regards the direct descent of corn from teosinte as a distinct possibility.

The theory of common ancestry maintains that corn originated from a perennial, wild, corn-like ancestor, now extinct, and that this extinct ancestor, sometimes called pre-maize, in turn had an ancestor, likewise extinct, in common with teosinte and Tripsacum; also that the native range of all of these species was Central America and Mexico. Actually the theory represents the application to the American *Maydeae* of the broad views of Darwin and earlier students of evolution.

The factual evidence claimed by the proponents of this theory falls into two categories. (A) The three groups—corn, teosinte and Tripsacum—are very similar, except that each has modifications of its own which have led to the differences now found among them. For example, teosinte and Tripsacum have lost one member of each original pair of pistillate spikelets, but corn has not; most varieties of corn and teosinte have lost the terminal staminate portion of the lateral inflorescence (ear), but Tripsacum has not. Weatherwax (41, 42) pointed out by way of explanation that, if we could restore to each of the three groups the primitive organs which have been modified in evolution, they would converge in a common type, giving us an idea of the common ancestor. But more revealing, in our opinion, is the result that would be obtained by restoring the primitive organs of only corn and Tripsacum, omitting teosinte. The common type towards which they would converge is the same as when teosinte is included. This fact is best explained by the hypothesis of the hybrid origin of teosinte, because this hypothesis holds that the characters of teosinte are merely a combination of those of corn and Tripsacum.

(B) It is stated that corn, teosinte and Tripsacum are

now sympatric only in Central America and Mexico, and for this reason all of them probably originated from a common ancestor which also occurred there. When the fallacy of placing such strong reliance on this present-day distribution is recognized, little or no factual evidence for the theory of common ancestry remains. Stebbins (36) reviews the literature on the theory that centers of diversity correspond to centers of origin. He points out that the theory has many pitfalls, except when the group in question is young and the selective forces of the environment have been operating in about the same manner throughout its evolutionary history. Stebbins shows that related genera, congeneric species and even conspecific populations might be expected to have widely disjunct ranges. He cites numerous examples of a single species with two ranges separated by half the distance around the earth. He shows also that examples of closely related disjunct taxa are not rare exceptions but are numerous and that some of them have been known since the time of Darwin.

Much of the validity of the Montgomery-Weatherwax theory depends upon the assumed correlation between the common ancestry and the common place of origin of the three groups. If one or two of the groups were shown to have originated elsewhere than in the present center of diversity (and this may yet prove to be true especially of Tripsacum), this would seriously weaken the theory. In addition, the proponents of the theory assume the previous existence of a pre-maize and of the common ancestor of pre-maize, teosinte and Tripsacum without one iota of evidence. The tripartite theory, in contrast, is more flexible and much less dependent upon completely unknown ancestors of corn. Indeed, it requires no ancestral types other than forms still in existence. Types of pod corn very similar to our hypothetical an-

cestor occur today; types of Tripsacum and corn which come extremely near to satisfying the requirements for the putative parents of teosinte are well known. Yet Weatherwax (41,42) states that it is the tripartite theory, rather than the "simple" theory of common ancestry, which "is topheavy with assumptions of such character that if one of them should be rejected the whole structure would fall."

The theory of common ancestry has two additional weaknesses which are serious: (A) It does not, Weatherwax's and Randolph's contentions to the contrary, notwithstanding, explain all of the known facts. (B) It can not easily be tested.

A. Some of the facts which the theory of common ancestry does not explain are discussed in detail in other papers of this series (23, 32). Here it will suffice to point out that the theory does not account for the facts that (a) teosinte is intermediate between maize and Tripsacum in a great majority of its characteristics (21, 31); (b) early archaeological maize is more "maize-like" than later maize (7, 11, 19, 20, 25); (c) fossil pollen of maize and Tripsacum were found at great depths at one site in Mexico, whereas teosinte pollen occurred only in the upper levels of the drill core; (d) forms of pod corn are now in existence which possess all of the characteristics expected in the ancestral form (16, 17); (e) variation in knob numbers is correlated with tripsacoid characteristics (18), and with proximity to Guatemala, the reputed center of origin of teosinte (21, 30).

B. The theory is largely untestable, because the only evidence which could prove it to be correct beyond a reasonable doubt would be the discovery of prehistoric remains, antedating agriculture, of all three groups of the American *Maydeae* and of the remote ancestor from which these three groups stem. Since it is largely untest-

able, it neither stimulates new research nor points to possible new methods of maize improvement. In this respect, the theory is less useful than the tripartite theory which has furnished the impetus for an extensive series of researches on maize and its relatives and has also suggested new possibilities for improving maize. If two theories appear to be equal in validity, the one which is testable and which stimulates new research is the more useful; a theory which is plausible but untestable tends to stifle research.

In emphasizing the differences between the tripartite theory and that of common ancestry it should not be overlooked that there are also important resemblances between them. The two theories agree that (a) corn is an American plant; (b) it is descended, with Tripsacum, from a remote common ancestor; (c) its immediate ancestor was a freely-branching plant bearing small ears with grains enclosed in glumes; (d) corn attained its present form through changes occurring during domestication, which began not more than a few thousand years ago. In a broad sense, then, the two theories agree with respect to the place, time and manner of origin. In the same broad sense, the problem of the origin of corn can almost be said to be solved.

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ERRATA

Page 65, line 13
for Sholz read Scholz

Page 105, line 19
for cornoso read carnoso

Page 106
add Drawn by Leslie A. Garay

Page 151, line 8
for basem read basim

Page 123, line 6
for lanceoloto read lanceolato

Page 172
reverse upper and lower legends

Page 278
after *Banisteriopsis inebrians* add *Banisteriopsis quitensis* (Ndz.) Morton, Colombia, Ecuador, Peru

Page 283, line 7
for *utilissima* read *esculenta*

Page 310, line 1
for florium read florum

Page 316, line 9
for *Hostmanii* read *Hostmannii*

Page 317, line 18
for *specimine* read *speciminis*

Page 317, line 26
for essensial read essential

Page 323, line 22
for Gary read Garay

Page 324, line 1
for (*Lehm.*) read (*Lem.*)

Page 325, line 8
for Barb. Rod. read Barb.-Rodr.

Page 375, line 14
for terminal read subterminal